LJ-93-01

FEB 12 1993

SOUTHWEST FISHERIES SCIENCE CENTER

NATIONAL MARINE FISHERIES SERVICE SOUTHWEST FISHERIES SCIENCE CENTER P.O. BOX 271 LA JOLLA, CA 92038

JANUARY 1993

LIBRARY

FEB 23 1993

National Marine Fisheries Service
2570 Dole Street
Honolulu, Hawaii

STATUS OF THE NORTHERN ELEPHANT SEAL POPULATION ALONG THE U.S. WEST COAST IN 1992

By

Jay Barlow, Peter Boveng, Mark S. Lowry,
Brent S. Stewart, Burney J. Le Boeuf, William J. Sydeman,
Ron J. Jameson, Sarah G. Allen, and Charles W. Oliver

ADMINISTRATIVE REPORT LJ-93-01

This Administrative Report is issued as an informal document to ensure prompt dissemination of preliminary results, interim reports and special studies. We recommend that it not be abstracted or cited.

NESASS.WP5 January 26, 1993

STATUS OF THE NORTHERN ELEPHANT SEAL POPULATION ALONG THE U.S. WEST COAST IN 1992

Jay Barlow[1]
Peter Boveng[2]
Mark S. Lowry[1]
Brent S. Stewart[3]
Burney J. Le Boeuf[4]
William J. Sydeman[5]
Ron J. Jameson[6]
Sarah G. Allen[5]
Charles W. Oliver[1]

[1]Southwest Fisheries Science Center
P.O. Box 271, La Jolla, CA 92038

[2]National Marine Mammal Laboratory
7600 Sand Point Way, N.E., Seattle WA 98115

[3]Hubbs-Sea World Research Institute
1700 South Shores Rd., San Diego, CA 92109

[4]Institute of Marine Sciences
University of California, Santa Cruz, CA 95064

[5]Point Reyes Bird Observatory
4990 Shoreline Highway, Stinson Beach, CA 94970

[6]U.S. Fish and Wildlife Service
P.O. Box 70, San Simeon, CA 93452

NOTE: Coauthors agreed to provide unpublished counts for this report under the condition that these data not be cited. Please do not cite.

ABSTRACT

Northern elephant seals (Mirounga angustirostris) are recovering from excessive hunting that caused a population crash in the late 19th century. The recovery began in Mexico, but current growth of the population is almost entirely in the U.S. Approximately 21,000 northern elephant seal pups were born at U.S. rookeries in 1991. Based on this and a demographic model of age structure, the total population size in the U.S. is estimated to be about 73,300 animals (range = 67,400-86,100). Conservatively, the minimum population size is the actual count of seals hauled out during the 1991 breeding season or approximately 42,800. Since 1981, births have increased 6.67% annually, and the population as a whole is assumed to be growing at the same rate. Dynamic response analysis of the 1964-91 time series of births suggests that the population is above its maximum net productivity level and may therefore be within the range of an optimum sustainable population (OSP). From that analysis we estimate that the population is at 77% of carrying capacity (K), with a bootstrap 95% confidence interval of 42% K to 112% K. Given these extremely broad confidence intervals and additional sources of uncertainty, little confidence can be placed on the estimate of 77% K or on the conclusion that the population is in the OSP range. Incidental mortality by humans is primarily associated with U.S. gillnet fisheries and was estimated as 137 seals in 1991.

INTRODUCTION

The northern elephant seal (Mirounga angustirostris) is one of several species of pinnipeds that inhabit Pacific coastal waters of the United States. Management and conservation of elephant seals are subject to the guidelines and regulations of the U.S. Marine Mammal Protection Act of 1972 and subsequent amendments. Management under the Act requires periodic assessment of the status of marine mammal populations. Such assessments were conducted previously by the National Marine Fisheries Service (NMFS 1980; Boveng 1988). This document is an update of Boveng (1988) and a synthesis of the current information on the status of the elephant seal population along the U. S. west coast.

History of Exploitation and Management

The exploitation and subsequent recovery of the northern elephant seal population was described in several papers (e.g., Bartholomew and Hubbs 1952; Bartholomew and Hubbs 1960; Le Boeuf and Panken 1977; Le Boeuf and Mate 1978; Stewart 1992; Stewart et al., in press). The seals were harvested extensively for oil in the 19th century. Bartholomew and Hubbs (1960) speculated that the entire species consisted of fewer than 100 individuals at the turn of the century. Genetic studies have shown a low level of genetic diversity in the northern elephant seal (Bonnell and Selander 1974;

Lehman, Wayne, and Stewart, in press), perhaps due to this population bottleneck. The Mexican government afforded protection to the species in 1922 (Bartholomew and Hubbs 1960), as did the U.S. a few years later (Le Boeuf and Panken 1977). Steady population growth, evidenced by colonization of new rookeries and haulouts (Allen, Peaslee, and Huber 1989; King 1989; Stewart et al., in press) and increasing numbers at existing rookeries (see below), has continued to the present, although some rookeries such as the South Farallon Islands have stabilized (Stewart et al., in press).

Life History of the Northern Elephant Seal

The northern elephant seal is the largest phocid in the northern hemisphere; females weigh up to 750 kg (Le Boeuf, Condit, and Reiter 1989) and males to 2300 kg (Deutsch, Haley, and Le Boeuf 1990). This species breeds along the Pacific coasts of California and Baja California, primarily on offshore islands. Typically, females give birth first when 3-5 years old (Le Boeuf, Whiting, and Gantt 1972; Reiter, Panken, and Le Boeuf 1981; Reiter and Le Boeuf 1991; Huber et al. 1991b; Sydeman et al. 1991), and the annual birth rate for mature females ranges from 0.79 to 0.92 for the Farallon Island population (Huber 1987). Weaning success increases log-linearly with female age (Reiter, Panken, and Le Boeuf, 1981, Sydeman et al. 1991). Reproductive senescence in female northern elephant seals is related to number of previous births rather than age (Sydeman et al. 1991). Survivorship of females is inversely related to age of primiparity; indications are that the fitness benefit of breeding at age 3 does not outweigh the cost of decreased survival (Reiter and Le Boeuf 1991). Males may become sexually mature by age 6 years and reach prime breeding condition at 9-12 years (Le Boeuf and Reiter 1988). Pregnant females come ashore to give birth from December through February; most births occur in January (Odell 1974; Stewart 1989; Sydeman et al. 1991). Seals mate approximately 24 days after parturition (Le Boeuf, Whiting, and Gantt 1972; Stewart 1989). When they are about 1 month old, pups are weaned and abandoned on the beaches (Odell 1974; Le Boeuf, Condit, and Reiter 1989; Stewart 1989). Pups go to sea 1-3 months later (Odell 1974; Reiter, Stinson, and Le Boeuf 1978). Older juveniles and adults return to the beaches from March to August to molt, and males return later than females (Orr and Poulter 1965; Odell 1974; Stewart and Yochem 1984; Stewart 1989). Great white sharks, Carcharodon carcharias, are the only know aquatic predator of elephant seals. At the Farallon Islands they prey predominantly on immature elephant seals (Ainley et al. 1985). An estimated 10-15% of immature seals that haulout at the Farallon Island rookery in the autumn are later killed by white sharks (Sydeman, PRBO, unpublished data). Yearly differences in immature survival (Huber et al. 1991b) indicate that food limitation also contributes to mortality in some years.

While at sea, adult males and females range widely north and west of their rookeries (DeLong, Stewart, and Hill 1992; Le Boeuf, in press; Stewart and DeLong, in press a&b). Females feed between 40° and 45° N latitude and out to 160° W longitude (Stewart and DeLong, in press a&b). Males travel even farther, feeding as far north as the eastern Aleutians and the northern part of the Gulf of Alaska (Stewart and DeLong 1990, in press a&b; Le Boeuf et al., in press). Modal dive depths are 300 to 700 m for females (Le Boeuf et al. 1986; Le Boeuf et al. 1989; Naito et al. 1989; Stewart and DeLong 1990, in press a&b) and 350 to 800 m for males (Stewart and DeLong 1990, in press; DeLong and Stewart 1991). Maximum recorded dive depths are 1567 m for females and 1581 m for males (Stewart and DeLong 1990; DeLong and Stewart 1991). Elephant seals are known to feed on mesopelagic squid and Pacific whiting (Antonelis et al., in press).

POPULATION AND STOCK STRUCTURE

Biological Basis of Populations

The entire population of northern elephant seals descended from a small group of animals at Isla de Guadalupe, Mexico around the turn of the century (Townsend 1899, Bartholomew and Hubbs 1960). Movement among islands is still common. Huber et al. (1991b) showed that, of females that were tagged as pups on the South Farallon Islands and were subsequently resighted, 15% had moved to San Miguel Island, San Nicolas Island, or Año Nuevo. There is no evidence of genetic differentiation between islands in California (Lehman, Wayne, and Stewart, in press). The reestablishment of breeding colonies on California islands and other documented movements of tagged seals (Le Boeuf, Ainley, and Lewis 1974; Bonnell et al. 1980; Condit and Le Boeuf 1984; Stewart, Yochem, and Huber 1985; Huber et al. 1986) indicate that genetic exchange between rookeries is frequent. Therefore, we think that it is reasonable to consider the entire species as a single population.

Recommended Stocks for Management

In this assessment, we consider elephant seals breeding in Mexico and in the U.S. as belonging to separate stocks. Although demographic and genetic exchange occurs between these stocks, they are probably small relative to the local reproduction in both countries. Information available on the Mexico stock is much less detailed than that available for the U.S. stock, making this stock division a practical necessity.

POPULATION SIZE

Estimation Methods

The life history of northern elephant seals precludes a complete census of the population because the animals ashore at any time represent only a portion of the total population. The spread in birth dates ensures that by the time numbers of adult females ashore have peaked, some females have already departed (Stewart 1989). The only age class that lends itself to a nearly complete census is the cohort of pups born in December, January, and February. Thus, pup counts are a useful index of population trends.

We estimated the total population size from the number of pups using a life-table approach. We constructed hypothetical schedules of survivorship separately for males and females and then, assuming a stable age distribution, computed the predicted age structure for a population growing at the recently observed annual rate of 8.41 percent (see POPULATION GROWTH RATES). Although local, short-term departures from a stable age distribution are probable, calculations of the average percentage of pups over the entire population is robust to this sort of violation in the assumption of stable age distribution. The assumed survivorship schedules were derived from those given by McCann (1985) for southern elephant seals (Mirounga leonina). The southern elephant seal survivorship schedules were fitted to non-linear, 5-parameter functions (Table 1) (Barlow and Boveng 1991) to facilitate an analysis of the sensitivity of the population estimate to variation in survival rates. The corresponding estimate of population size is 3.72 times the number of female pups plus 3.26 times the number of male pups. The sex ratio at birth is assumed to be unity [measured values of percent male are 51.2% at birth and 49.6% at weaning (Le Boeuf, Condit, and Reiter 1989) and 50.7% at birth and 50.8% at weaning (Stewart 1989)]; therefore, population size is estimated as 3.49 times the total number of pups (males and females).

Population Estimates

Births north of Mexico occur at San Miguel Island, San Nicolas Island, Año Nuevo, South Farallon Islands, San Clemente Island, Santa Rosa Island, Cape San Martin, and Point Reyes Headland (Table 2). Some counts for these rookeries include direct counts of dead pups. Most others include corrections for the expected number of dead pups based on site-specific mortality rates (Stewart 1989). Two independent pup counts were available for some years on San Miguel, San Nicolas, and Santa Rosa Islands. If both counts were made between January 25 and February 25, we averaged the estimates to arrive at consensus estimates of total pups born; consensus estimates are used in subsequent figures and analyses. In general, differences between counts were less than 10%; however, two counts at San Nicolas Island in 1991 differed by approximately 12%.

Clearly, a detailed analysis of the differences between counts would provide useful information about the precision of individual counts. The total births in 1991 for California was approximately 21,000. Using the multiplier of 3.49, the total U. S. elephant seal population size was an estimated 73,300 at the end of the 1991 breeding season.

Stewart (1980) estimated that the total elephant seal population size just after the pupping season was 3.6 times the number of pups born. His estimate assumed that all mature females bear a pup, that breeding age males are 0.3 times as numerous as mature females, and that the number of immature animals (excluding pups) is equal to the number of matures. Le Boeuf and Bonnell (1980) used a factor of 4 to convert from counts of pups born to total population size. Thus, independent researchers estimate the total population size of northern elephant seals as approximately 3.5 to 4 times the pup count (see Stewart et al., in press).

For southern elephant seals, McCann (1985) used a factor of 4.5 to estimate total population size from the number of pups (actually he used 3.5 times the number of pups to yield the number of non-pups, which is equivalent). We based our estimate of the fraction of pups in the northern elephant seal population on the same survivorship schedule on which McCann based his calculation. The difference between McCann's result and ours is explained by differences in population growth rates between the two populations. A high population growth rate for northern elephant seals (8.41%) skews the age distribution to give a higher fraction of pups relative to the southern species (which had an assumed growth rate of zero).

To investigate the sensitivity of the population estimate to assumptions about survival rates, the survivorship curves were scaled by various values of longevity (defined as the 99th percentile of the age distribution) (Barlow and Boveng 1991). This estimated longevity was 16 years for females and 14 years for males based on the life tables by McCann (1985) for southern elephant seals. Scaling by a smaller value for longevity is equivalent to decreasing the survival rate at each age; conversely, greater longevity values imply higher survival rates. If the longevity is 13 years for both females and males, the population sizes would be 3.31 and 3.12 times the number of female and male pups (respectively) for a total population estimate of 67,400. If the longevity is 20 years for both females and males, the population sizes would be 4.20 and 4.01 times the number of female and male pups (respectively) for a total population estimate of 86,100. Quantitative estimates of longevity are difficult to obtain for northern elephant seals, but several sources of evidence support our use of the range of 13-20 years. Le Boeuf and Reiter (1988) calculate an age at 1% survivorship of approximately 13 years for males and females based on a number of assumptions regarding tag loss. However, female elephant seals known to be older than 13

years have commonly been observed at Año Nuevo (Reiter, Panken, and Le Boeuf 1981) and the Farallon Islands (Huber et al. 1991b, Sydeman et al. 1991). Huber et al. (1991) found one 16 year old female in a very small cohort that had been observed for 16 years. She also cited a case of an 18 year old female northern elephant seal (B. Stewart cited as pers. comm. in Huber et al. 1991b). Although uncommon, females up to 20 years of age and males up to 14 years have been seen at Año Nuevo (Le Boeuf, pers. observ.). In recent years, several 18 year old females and one that was at least 21 years have been seen on the South Farallon Islands (Sydeman and PRBO, unpublished data). Existing data support our assertion that the age at 1% survivorship is probably greater than or equal to 13 years. The extreme rarity of specimens surviving to age 20 supports our use of this as a maximum estimate for longevity. Because 13-20 years represent extremes in plausible longevities for this species, the true population size in California is probably not greater than 85,800 or less than 67,200.

In Mexico, Le Boeuf and Bonnell (1980) estimated the total population size as 35,000. Stewart et al. (in press) estimate the number of pups born in Mexico in 1991 as 7,015+, but that estimate does not include Islas San Benito Oeste or Este. A Mexican researcher, Pablo Loreto C., counted 381 pups on San Benito Oeste in 1991 (L. Fleischer, pers. comm.). Because the Mexican population appears to be growing very slowly (see POPULATION GROWTH RATES), the 4.5 multiplier used by McCann (1985) is appropriate to extrapolate from number of births to the number in the entire population. Based on this, we estimate that the population in Mexico was at least 33,200 in 1991.

Minimum Population Estimate

Insufficient information exists to estimate a lower 95% confidence interval on the life-table-based population estimate. Instead, we estimate minimum population size as the actual count of individuals during breeding season. The actual count of elephant seals at the principal rookeries (San Miguel Island, San Nicolas Island, Santa Rosa Island, San Clemente Island, the Farallon Islands, Año Nuevo, and Point Reyes) in 1991 is 42,177 (Table 3). The total numbers hauled out in 1991 at Santa Barbara Island and Cape San Martin have not been obtained but can be estimated conservatively as follows: multiply the pup count by 2 (to account for pups and their mothers) and add 0.170 times the pup count to account for the average number of adult males hauled out during breeding season (based on the principal rookeries, Table 3). The minimum estimate of population size is thus 42,177 plus 2.170 times 308 or an estimated 42,845 northern elephant seals on the beach during breeding season.

POPULATION GROWTH RATES AND TRENDS

Trends in Abundance

Elephant seal abundance in California has been increasing since 1965 (Fig. 1). Cooper and Stewart (1983) found that births at California rookeries increased at rates ranging from 13.6 to 53.3 percent per year and at an average rate of about 14.5 percent during the period 1965-1977. They also estimated that the combined U.S./Mexican population grew at about 8.3 percent annually between 1965 and 1977. The rate of growth of the total California breeding population during recent years is estimated below.

From a regression of the natural logarithm of the pup count on year of the count, the average rate of growth in total California pup counts was 11.5 percent annually between 1964 and 1991 (slope=0.1085, s.e.=0.0052, $P<<0.001$, $R^2=0.970$). Because pup counts for the years 1964-79, 1980-85, and 1987-91 seem to follow different slopes (Fig. 2), we performed separate regressions for each period. The estimated rate of growth for 1964-79 was 14.9%, for 1980-85 was 10.2%, and for 1987-91 was 8.41%. Slopes for these periods are significantly different (analysis of covariance, $p < 0.001$); however, the last two periods do not differ significantly in slope ($p=0.2$).

The limited data available suggest that the Mexican population is stable or, at least, is growing more slowly than the U. S. population (Cooper and Stewart 1983; Stewart et al., in press). The dominant rookery in Mexico on Guadalupe has stopped growing and may have declined slightly since the 1970s (Le Boeuf and Bonnell 1980; Le Boeuf, Gallo-Reynoso, and Figueroa-Carranza 1992; Stewart et al., in press). Data for Isla San Benito Oeste, Baja California shows relatively stable pup counts from 376 in 1965 (Rice, Kenyon, and Lluch 1965) to 381 pups in 1991 (L. Fleischer pers. comm.). Le Boeuf, Gallo-Reynoso, and Figueroa-Carranza (1992) concluded that elephant seals are slowly increasing in number on Islas San Benito and Cedros. Until a complete census is made at Islas San Benito, it will not be possible to estimate population growth rates in Mexico.

Berkson and DeMaster (1985) used a model to investigate the reliability of pup counts as an index for rates of change in the entire population. They found that the rate of change in pup counts may be a biased estimator of total population change and that the direction of the bias depends on the relative timing of density-dependent pup survival and the census. When the primary density-dependent process in their model was adult survival, the bias was small. Elephant seal pup mortality between birth and weaning may be density dependent at extremely high densities (Reiter, Panken, and Le Boeuf 1981, Reiter and Le Boeuf 1991), but the effect has not been demonstrated on the largest rookeries (San Miguel and San Nicolas, Stewart 1989). Also, the probability of a pregnant female hauling out to pup on a particular rookery may be density dependent

(Reiter, Panken, and Le Boeuf 1981). Thus, for a particular rookery there may be density-dependent processes both preceding and following the pup census. However, the extent to which these density-dependent processes are regulating the total number of pups is not known well enough to predict the magnitude or direction of bias in the estimated growth rate.

Growth Rates at MNPL

Because populations are estimated to have only recently increased above their maximum net productivity level (MNPL) (the population achieved 50% of their estimated carrying capacity circa 1984, see below), the growth rate at the MNPL can be estimated as the growth rate over the last decade (6.67% per year, 1981-1991).

STOCK STATUS RELATIVE TO OSP AND K

OSP Determination

Because the historical harvest of northern elephant seals is unknown, back calculation could not be used to estimate the status of northern elephant seals. Therefore, we use dynamic response analysis (Goodman 1988; Gerrodette 1988; Gerrodette and DeMaster 1990) based on pup counts to assess the status of the elephant seal stock relative to its maximum net productivity level (MNPL). A population is assumed to be at optimum sustainable population (OSP) level if it is greater than its MNPL.

In a previous assessment, Boveng (1988) used two forms of the dynamic response technique to estimate the status of the elephant seal population relative to its MNPL. Recent findings (Eberhardt 1992; Boveng, unpublished) suggest that the form of dynamic response analysis that uses a measure of curvature in the time-trajectory of abundance (DeMaster et al. 1982; Boveng, DeMaster, and Stewart 1988, Boveng 1988) lacks statistical power and can be overly sensitive to environmental perturbations. The presence of large El Niño perturbations in the time series of elephant seal pup counts (Stewart and Yochem 1991) invalidates this time-trajectory approach. Here we use only the more general form of dynamic response that relies on estimates of per-capita production to infer population status relative to MNPL. The general form of the dynamic response method, as proposed by Goodman (1988), is based on local analysis of the slope of the relationship between per-capita production and stock size, evaluated at current stock size. We estimated per-capita production in year i (P_i) as the n-th root of (N_{i+n}/N_i) minus 1.0, where n is the time until the next available count (typically 1 year). To the extent that pup counts are correlated with total stock size, this estimate of production is unbiased (Goodman 1988). We recognize, however, that an error is associated with the pup counts as indices of abundance and assume here that the resulting biases in production estimates are negligible.

Assessing the status of a population relative to its MNPL requires estimating the slope of the tangent line to the per-capita production curve at N^*, the stock size of interest (Goodman, 1988). The slope, α, of the tangent line is obtained by evaluating the derivative of the per-capita production curve at N^*. The slope and the observed per-capita production associated with N^* define a straight line that intercepts the production axis at some value, say ß. As shown by Goodman (1988), if $N^* > -ß/2\alpha$, the stock size N^* is above MNPL, if $N^* = -ß/2\alpha$ then N^* is equal to the MNPL, and if $N^* < -ß/2\alpha$, N^* is below MNPL.

It is not a simple matter to choose a model for fitting or smoothing the per-capita production curve. Because the analysis of the shape of the production curve is intended to be "local" (i.e., in the range of stock sizes near the size of the stock in question) the model need not have a mechanistic or population theoretical basis, provided the model adequately describes the shape for the range of stock size of most concern. We used a cubic spline method to fit the production data and a jackknife cross-validation method for choosing the value of the spline smoothing parameter (Silverman 1985). The smoothing parameter that minimized the cross-validation error was one that implied a linear regression fit (Fig. 3, Table 4). Thus, the dynamics of the northern elephant seal population resemble those predicted by the simple logistic growth model with a maximum net productivity level at approximately 50% of K.

The linear regression is a fit to the model:

$$P = r\{1 - (N/K)\} \qquad (2).$$

For this model, the first derivative with respect to stock size (N) is

$$dP/dN = -r/K \qquad (3).$$

This derivative is a constant; therefore, α is equal to $-r/K$ for any stock size. Similarly ß is equal to r for any stock size. The quantity $-ß/2\alpha$ then is equal to K/2, as expected for a simple logistic growth model. The estimate of K for the elephant seal data is that population that would result in 27,377 births (Table 4). Bootstrap 95% confidence intervals on this estimate (18,718-49,527) were calculated by randomly selecting data points from Figure 3 (with replacement), estimating the x-intercept, repeating this process 1000 times, and selecting the 25th and 975th ranked values. The most recent number of births (20,972) is equal to about 77% K and is substantially greater than 13,685 (K/2), indicating that the population dynamics are similar to those of a population at levels above MNPL.

The conclusion that northern elephant seals are above their MNPL is far from certain. In addition to the uncertainty expressed in the wide confidence intervals, two other factors should be

considered. First, the very high rates of production seen in early years (Table 4) are likely to be inflated somewhat by immigration from Mexico. The apparent decline in production may be due to a lower proportional contribution by immigration as the California population increased. Using a randomization test for density dependence (Pollard, Lakhani, and Rothery 1987), the 1980-91 time series does not show any evidence of density dependence ($p = 0.22$). Much of the apparent density dependence in the longer 1964-91 time series may be the result of pre-1980 immigration. Second, the 1985/86 datum (the only negative datum) is likely to be very influential in the regression. The negative value is likely to have been caused by the low number of newly mature females from a cohort (or cohorts) with high pup mortality on San Miguel and San Nicolas Islands (Stewart and Yochem 1991) and at Año Nuevo and Cape San Martin (Le Boeuf and Reiter 1991) during the 1982/83 El Niño. Although not an outlier in the sense of representing an unnatural perturbation, this may be a once-per-century phenomenon. Excluding this point, an estimated 32,241 births would occur annually at carrying capacity, and the current abundance is an estimated 59% K. Both of these factors may cause the northern elephant seal population to appear closer to carrying capacity than it really is.

Stewart (1989) conducted an equivalent to a dynamic response analysis by fitting a non-linear (θ-Logistic, Gilpin, Case, and Ayala 1976) model to the time series of pup counts at one rookery (Pt. Bennett, San Miguel Island). The resulting fit indicated that, for that rookery, the maximum net growth rate occurs at 75% of K. Stewart concluded that, with respect to one resource (suitable breeding space), northern elephant seals would be expected to have a maximum net productivity level that is greatest near K. If, as our analyses suggest, maximum net productivity occurs at 50% K, this may indicate that suitable breeding space is not limiting the elephant seal population. Alternatively, as MacCall (1983) showed for northern anchovies that, given habitat heterogeneity, the maximum net growth rate for an entire population is expected to occur at a lower fraction of carrying capacity than the maximum net growth rate evaluated for a local population. We see a similar pattern for elephant seals, with the maximum net growth rate of the California population occurring at a lower fraction of K (50%) than the maximum net growth rate of the Pt. Bennett rookery (75%).

Condition Indices

It is likely that as elephant seals approach carrying capacity measurable changes will occur in the condition of individuals. Evidence of such changes can be used to make inferences about the status of the population (Eberhardt and Siniff 1977; DeMaster 1984). The type of changes are likely to depend on what factors are important in determining carrying capacity. Factors which might be important include resource depletion, physical crowding on rookeries, and disease.

The 1982/83 El Niño provides insight into how resource depletion affects elephant seal populations. El Niño had the effect of temporarily reducing resources for most pinnipeds in the eastern Pacific (Trillmich and Ono 1991). Its effect on elephant seals was similar to, though perhaps not as intense as, its effect on other pinniped species (Trillmich et al. 1991). Pre-weaning pup mortality increased very dramatically in 1983, but this was the direct result of storms associated with El Niño and not resource depletion (Le Boeuf and Reiter 1991; Huber, Beckham, and Nisbet 1991a; Stewart and Yochem 1991). Post-weaning pup and juvenile mortality increased at the South Farallon Islands and Año Nuevo rookeries (Le Boeuf and Reiter 1991; Huber, Beckham, and Nisbet 1991a) and probably were associated with a reduced availability of resources. The time females spent at sea between pupping and molting increased at San Nicolas Island and Año Nuevo (Stewart and Yochem 1991), which was also probably related to a lack of resources. The natality rate of all female age classes decreased in the 2 post-El Niño years at the South Farallon Islands (Huber, Beckham, and Nisbet 1991a), probably indicating that resource depletion had a lasting effect.

If El Niño can be viewed as a model of the general effect of resource depletion on northern elephant seals, approach to carrying capacity may be indicated by an increase in juvenile mortality, an increase in foraging time for females, and a decrease in age-specific natality. To date, changes in these parameters have not been detected except in association with El Niño. Density-dependent effects may be manifest only in years of poor conditions. It will be important to monitor these parameters as elephant seal populations grow.

Other Information Bearing on Status

The present size of the northern elephant seal population may be greater than historic (pre-commercial-exploitation). One hypothesis is that mainland breeding was limited by large terrestrial predators and aboriginal human hunters (Le Boeuf and Panken 1977). Also, Stewart et al. (in press) reviewed archaeological studies that revealed a change in the species composition of pinniped remains in recent layers of Indian kitchen middens on the Channel Islands, leading them to suggest that over-exploitation may have occurred and that elephant seals may be more abundant now than they have ever been since the appearance of humans in the region. If these hypotheses are true, then both the present population and the present MNPL might be larger than the size of the population when non-aboriginal exploitation began in the early 19th century.

CURRENT BIOLOGICAL REMOVALS

Incidental Takes

Observations and studies of marine mammal mortality in U.S. commercial fishing operations revealed that elephant seal mortality was low, especially when compared with the mortality of California sea lions and harbor seals in the same area (NMFS 1980; Antonelis and Fiscus 1980; Miller, Herder, and Scholl 1983; Condit and Le Boeuf 1984; Wild 1985, 1986; Bishop 1985; Collins et al. 1984; Collins, Vojkovich, and Reed 1985; Collins et al. 1986; Diamond, Hanan, and Scholl 1986a; Diamond, Hanan, and Scholl 1986b; Diamond, Scholl, and Hanan 1987; Barlow et al. 1990). Quantitative estimates of elephant seal mortality based on a U.S. fishery observer program were first made in 1991. Total elephant seal mortality in California drift and set gillnet fisheries was estimated as 234 for the second half of 1990 (Lennert, Kruse, and Beeson 1991) and 137 in calendar year 1991 (Perkins, Barlow, and Beeson 1992). Mexico has an additional 35 drift gillnet vessels which fish similarly to the U.S. drift net vessels and which presumably take elephant seals (D. Hanan, pers. comm.). In non-U.S. fisheries, zero northern elephant seals were reported caught in the Japanese high-seas gillnet fishery for neon squid based on observations of 4% of the fleet's fishing effort in 1989 (Larntz, Garrott, and Jones 1991), and in the eastern North Pacific and Bering sea, only one elephant seal was reported taken by foreign fishing vessels during 1978-81 (Perez and Loughlin 1991). No northern elephant seals were taken in the 1988 experimental driftnet fishery for sharks in Oregon and Washington (Stick and Hreha 1989).

Subsistence Take

Currently, there is no subsistence take of northern elephant seals; however, archeological records show that there was in the past (Stewart et al., in press).

Illegal Killing

No information is available about other, illegal killing of northern elephant seals.

Research and Live Capture

Four northern elephant seals were reportedly killed accidentally in research since 1990 (I. Lagomarsino, pers. comm.). Four were killed intentionally for scientific research in the early 1980s. There have been no recent removals for public display.

Entanglement

Stewart and Yochem (1985, 1987, 1990) documented the frequency

of elephant seal entanglement (either seals with net or line fragments or with scars from previous entanglement) in surveys of San Miguel and San Nicolas Islands between 1983 and 1986. Approximately 0.15% of elephant seals observed in 1983 and 1984 were entangled and an additional 0.09% had scars, possibly caused by previous entanglement. In 1985 and 1986, about 0.16% were entangled and 0.20% scarred. One northern elephant seal was observed entangled in net fragments on San Clemente Island since studies began in 1981 (Oliver 1991b). Of those entangled in fishing net, it is not known whether they were caught in active or derelict fishing gear.

ACKNOWLEDGEMENTS

We thank L. Fleischer and P. Loreto C. for unpublished estimates of pup production on Isla Benito Oeste. This manuscript improved from reviews by D. DeMaster, T. Gerrodette, and the Pacific Pinniped Status Review Panel. W. Sydeman's participation is Contribution Number 552 from the Point Reyes Bird Observatory.

LITERATURE CITED

Ainley, D. G., R. P. Henderson, H. R. Huber, R. J. Boepelheide, S. G. Allen, and T. L. McElroy. 1985. Dynamics of white shark/pinniped interactions in the Gulf of the Farallons. Southern California Acad. Sci., Memoirs 9:109-122.

Allen, S. G., S. C. Peaslee and H. R. Huber. 1989. Colonization by northern elephant seals of the Point Reyes Peninsula, California. Mar. Mamm. Sci. 5:298-302.

Antonelis, G. A. and C. H. Fiscus. 1980. The pinnipeds of the California current. CalCOFI Report, Vol. XXI pp. 68-78.

Antonelis, G. A., S. Leatherwood, and D. K. Odell. 1981. Population growth and censuses of the northern elephant seal, Mirounga angustirostris, on the California Channel Islands, 1958-1978. Fishery Bulletin 79:562-563.

Antonelis, G. A., M. S. Lowry, C. H. Fiscus, B. S. Stewart, and R. L. DeLong. (in press). Diet of the northern elephant seal. In: B. J. LeBoeuf and R. M. Laws (eds.) Elephant Seals. U. C. Press, Berkeley.

Barlow, J., R. W. Baird, J. E. Heyning, K. Wynne, A. M. Manville II, L. F. Lowry, D. Hanan, J. Sease, and V. N. Burkanov. 1990. A review of cetacean mortality in coastal fisheries along the west coast of the U.S. and Canada and the east coast of the U.S.S.R. Working paper SC/90/G28 presented to the IWC Workshop on Mortality of Cetaceans in Passive Fishing Nets and Traps, La Jolla, CA, Oct 22-25, 1990. 48pp.

Barlow, J. and P. Boveng. 1991. Modelling age-specific mortality for marine mammal populations. Marine Mammal Sci. 7(1):84-119.

Bartholomew, G. A. and R. A. Boolootian. 1960. Numbers and population structure of the pinnipeds on the California Channel Islands. J. Mamm. 41:366-375.

Bartholomew, G. A. and C. L. Hubbs. 1952. Winter populations of pinnipeds about Guadalupe, San Benito, and Cedros Islands, Baja California. Journal of Mammalogy 33:160-171.

Bartholomew, G. A. and C. L. Hubbs. 1960. Population growth and seasonal movements of the northern elephant seal, Mirounga angustirostris. Mammalia 24:313-324.

Berkson, J. M. and D. P. DeMaster. 1985. Use of pup counts in indexing population changes in pinnipeds. Canadian Journal of Fisheries and Aquatic Sciences 42:873-879.

Bishop, J. B. 1985. Summary report of gill and trammel net

(set-net) observations in the vicinity of Morro Bay, California. Marine Mammal Commission Contract no. MM2629900-2. NTIS PB85-150076.

Bonnell, M. L., B. J. Le Boeuf, M. O. Pierson, D. H. Dettman, G. D. Farrens, C. B. Heath, R. F. Gantt, and D. J. Larsen. 1980. Pinnipeds of the Southern California Bight. In Marine Mammal and Seabird Surveys of the Southern California Bight Area 1975-1978. Vol. 3, Investigator's Reports, Part 1. 535 pp. NTIS PB81-248-71.

Bonnell, M. L. and R. K. Selander. 1974. Elephant seals: genetic variation and near extinctions. Science 184:908-909.

Boveng, P. 1988. Status of the northern elephant seal population on the U.S. West Coast. Southwest Fisheries Center Admin. Rep. LJ-88-05.

Boveng, P., D. P. DeMaster, and B. S. Stewart. 1988. Dynamic response analysis III. A consistency filter and application to four northern elephant seal colonies. Marine Mammal Science 4(3):210-222.

Collins, R. A., M. M. Vojkovich, A. R. Hartmann, and R. J. Reed. 1984. Progress report: Southern California nearshore gill and trammel net study, 1983. California Department of Fish and Game, Marine Resources Branch, Long Beach, California 90813.

Collins, R. A., M. M. Vojkovich, and R. J. Reed. 1985. Progress report: Southern California nearshore gill and trammel net study, 1984. California Department of Fish and Game, Marine Resources Branch, Long Beach, California 90813.

Collins, R. A., M. M. Vojkovich, R. J. Reed, and K. A. Hieb. 1986. Progress report: Southern California nearshore gill and trammel net study, 1985. California Department of Fish and Game, Marine Resources Branch, Long Beach, California 90813.

Condit, R. S. and B. J. Le Boeuf. 1984. Feeding habits and feeding grounds of the northern elephant seal. Journal of Mammalogy 65(2)281-290.

Cooper, C. F. and B. S. Stewart. 1983. Demography of northern elephant seals, 1911-1982. Science 219:969-971.

DeLong, R. L. and B. S. Stewart. 1991. Diving patterns of northern elephant seal bulls. Mar. Mamm. Sci. 7(4):369-384.

DeLong, R. L., B. S. Stewart, and R. D. Hill. 1992. Documenting migrations of northern elephant seals using day length. Mar. Mamm. Sci. 8(2):155-159.

DeMaster, D. P. 1984. A review of density dependence in marine mammals. Proceeding of the Workshop on Biological Interactions among Marine Mammals and Commercial Fisheries in the Southeastern Bering Sea. Alaska Sea Grant Report 84-1, pp. 139-148.

DeMaster, D. P., D. J. Miller, D. Goodman, R. L. DeLong and B. S. Stewart. 1982. Assessment of California sea lion fishery interactions. In Transactions of the 47th North American Wildlife and Natural Resources Conference, 1982. Wildlife Management Institute, Washington, D. C.

Deutsch, C. J., M. P. Haley, and B. J. Le Boeuf. 1990. Reproductive effort of male northern elephant seals: estimates from mass loss. Can. J. Zool. 68(12):2580-2593.

Diamond, S., D. Hanan, and J. Scholl. 1986a. Drift gill net observations for the 1983-1984 fishing season. In California Department of Fish and Game Coastal Marine Mammal Study, Annual Report for the Period July 1, 1983 - June 30, 1984. Administrative Report LJ-86-16, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California 92038.

Diamond, S., D. Hanan, and J. Scholl. 1986b. Drift gill net observations for the 1984-1985 fishing season. In California Department of Fish and Game Coastal Marine Mammal Study, Annual Report for the Period July 1, 1984 - June 30, 1985. Administrative Report LJ-86-25C, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California 92038.

Diamond, S., J. Scholl, and D. Hanan. 1987. Drift gill net observations for the 1985-1986 fishing season. Administrative Report SWR 87-4, National Marine Fisheries Service, Southwest Region, Terminal Island, California 90731.

Eberhardt, L. L. 1992. An analysis of procedures for implementing the dynamic response method. Mar. Mamm. Sci. 8(3):201-212.

Eberhardt, L. L. and D. B. Siniff. 1977. Population dynamics and marine mammal management policies. J. Fish. Res. Bd. Can. 34(2):183-190.

Gerrodette, T. 1988. Dynamic response analysis. II. Evaluation of dynamic response analysis in a simulated no-harvest case. Marine Mammal Science 4(3):196-209.

Gerrodette, T. and D. P. DeMaster. 1990. Quantitative determination of optimum sustainable population level. Mar. Mamm. Sci. 6(1):1-16.

Gilpin, M. E., T. J. Case, and F. J. Ayala. 1976. θ-selection. Mathematical Biosciences 32:131-139.

Goodman, D. 1988. Dynamic response analysis. I. Qualitative estimation of stock status relative to maximum net productivity level from observed dynamics under harvest. Marine Mammal Science 4(3):183-195.

Huber, H. R. 1987. Natality and weaning success in relation to age of first reproduction in northern elephant seals. Canadian Journal of Zoology. 65:1311-1316.

Huber, H. R., L. Fry, A. Rovetta, S. Johnston and J. Nusbaum. 1986. Studies of marine mammals at the Farallon Islands, 1983-1985. National Marine Fisheries Service, Administrative Report LJ-86-17C. Southwest Fisheries Center, La Jolla, California.

Huber, H. R., C. Beckham, and J. Nisbet. 1991a. Effects of the 1982-83 El Niño on northern elephant seals on the South Farallon Islands, California. pp. 217-233 In: F. Trillmich and K. A. Ono (eds.). Pinnipeds and El Niño. Springer-Verlag, Berlin.

Huber, H. R., A. C. Rovetta, L. A. Fry, and S. Johnston. 1991b. Age-specific natality of northern elephant seals at the South Farallon Islands, California. J. Mamm. 72(3):525-534.

King, J. E. 1989. New mainland haul-out site for the northern elephant seal, Mirounga angustirostris, in central California. California Fish and Game 75(4):244-247.

Larntz, K., R. A. Garrott, and L. Jones. 1991. Analysis of bycatch of selected bird and mammal species in the 1989 Japanese neon squid fishery. Unpubl. Manuscript.

Le Boeuf, B. J. 1977. Back from extation? Pacific Discovery 30:1-9.

Le Boeuf, B. J. (in press). Variation in the diving pattern of northern elephant seals with age, mass, sex, and reproductive success. In: B. J Le Boeuf and R. M. Laws (eds.). Elephant Seals. Univ. of Calif. Press, Berkeley.

Le Boeuf, B. J., D. G. Ainley, and T. J. Lewis. 1974. Elephant seals of the Farallones: population structure of an incipient breeding colony. J. Mamm. 55:370-385.

Le Boeuf, B. J. and M. J. Bonnell. 1980. Pinnipeds of the California Channel Islands: abundance and distribution. In D. Power (Ed.), The California Islands: Proceedings of a Multidisciplinary Symposium, pp. 475-493. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Le Boeuf, B. J. and K. T. Briggs. 1977. The cost of living in a seal harem. Mammalia 41:167-195.

Le Boeuf, B. J., R. Condit, and J. Reiter. 1989. Parental investment and the secondary sex ratio in northern elephant seals. Behav. Ecol. Sociobiol. 25:109-117.

Le Boeuf, B. J., D. P. Costa, A. C. Huntley, G. L. Kooyman and R. W. Davis. 1986. Pattern and depth of dives in northern elephant seals, Mirounga angustirostris. Journal of the Zoological Society of London 208:1-7.

Le Boeuf, B. J., D. Crocker, S. Blackwell, and P. Morris. (in press). Sex differences in diving and foraging behaviour of northern elephant seals. In: I. Boyd (ed.). Recent Advances in Marine Mammal Science. Oxford Univ. Press.

Le Boeuf, B. J., J. P. Gallo-Reynoso, and A. Figueroa-Carranza. 1992. Status of the northern elephant seal in Mexico. Abst. XVII Reunion Internacional para el Estudio de Los Mamiferos Marinos, April 21-25, La Paz, B.C.S., Mexico.

Le Boeuf, B. J. and B. R. Mate. 1978. Elephant seals colonize additional Mexican and Californian islands. Journal of Mammalogy 59:621-622.

Le Boeuf, B. J., Y. Naito, A. C. Huntley, and T. Asaga. 1989. Prolonged, continuous, deep diving by northern elephant seals. Can. J. Zool. 67:2514-2519.

Le Boeuf, B. J. and K. J. Panken. 1977. Elephant seals breeding on the mainland in California. Proceedings of the California Academy of Sciences 41:267-280.

Le Boeuf, B. J. and J. Reiter. 1988. Lifetime reproductive success in Northern elephant seals. pp. 344-362. In T. H. Clutton-Brock (ed.). Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems. U. Chicago Press.

Le Boeuf, B. J. and J. Reiter. 1991. Biological effects associated with El Niño Southern Oscillation, 1982-83, on northern elephant seals breeding at Año Nuevo, California. pp. 206-218 In: F. Trillmich and K. A. Ono (eds.). Pinnipeds and El Niño. Springer-Verlag, Berlin.

Le Boeuf, B. J., R. J. Whiting, and R. F. Gantt. 1972. Perinatal behavior of northern elephant seal females and their young. Behavior 43:121-156.

Lehman, N., R. K. Wayne, and B. S. Stewart. (in press). Comparative levels of genetic variability in harbor seals and

northern elephant seals as determined by genetic fingerprinting. In I. L. Boyd (ed.). Recent Advances in Marine Mammal Science. Symposia of the London Zool. Soc., Oxford Univ. Press.

Lennert, C., S. Kruse, and M. Beeson. 1991. Preliminary report on incidental marine mammal bycatch in California gillnet fisheries. Int. Whal. Commn working paper SC/43/03.

Lowry, M. S., L. J. Hansen, and S. D. Hawes. 1987. California sea lion and northern elephant seal pup counts and tagging data at Santa Barbara Island, California, from June 1983 through July 1986. Administrative Report LJ-87-03. National Marine Fisheries Service, Southwest Fisheries Center, P. O. Box 271, La Jolla, California, 92038. 19pp.

Lowry, M. S., W. L. Perryman, M. S. Lynn, and R. L. Westlake. 1992. Using large format vertical aerial photography to census northern elephant seals (Mirounga angustirostris) at San Miguel, San Nicolas, and Santa Rosa Islands, California. Administrative Report LJ-92-20. National Marine Fisheries Service, Southwest Fisheries Center, P. O. Box 271, La Jolla, California, 92038. 31pp.

Mate, B. R. 1977. Aerial censusing of pinnipeds in the eastern Pacific for assessment of population numbers, migratory distributions, rookery stability, breeding effort, and recruitment. Final report to U.S. Marine Mammal Commission, Washington, D.C. NTIS PB-265 859.

MacCall, A. 1983. Population models of habitat selection, with application to the northern anchovy. Ph.D. Dissertation. University of California, San Diego. 98pp.

McCann, T. S. 1985. Size, status and demography of southern elephant seal (Mirounga leonina) populations. In J. K. Ling and M. M. Bryden (eds.), Studies of Sea Mammals in South Latitudes. South Australian Museum. 132 pp.

Miller, D. J., M. J. Herder, and J. P. Scholl. 1983. California marine mammal-fishery interaction study, 1979-1981. Administrative Report LJ-83-13C. National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

Naito, Y., B. J. Le Boeuf, T. Asaga, and A. C. Huntley. 1989. Preliminary analysis of long term continuous diving in female elephant seals, Mirounga angustirostris. Ant. Rec. 33:1-9.

NMFS, 1980. A report based on the workshop on stock assessment and incidental take of marine mammals involved in commercial fishing operations. National Marine Mammal Laboratory,

Northwest and Alaska Fisheries Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, Washington 98115.

Odell, D. K. 1971. Censuses of pinnipeds breeding on the California Islands. Journal of Mammalogy 52:187-190.

Odell, D. K. 1974. Seasonal occurrence of the northern elephant seal, Mirounga angustirostris, on San Nicolas Island, California. Journal of Mammalogy 55:81-95.

Oliver, C. W. 1991a. 1986-1987 field studies on pinnipeds at San Clemente Island, California. Southwest Fisheries Center Administrative Rep. LJ-91-24, La Jolla, CA. 31pp.

Oliver, C. W. 1991b. 1988-1991 field studies on pinnipeds at San Clemente Island, California. Southwest Fisheries Center Administrative Rep. LJ-91-27, La Jolla, CA. 33pp.

Oliver, C. W. and M. S. Lowry. 1987. Pinniped studies conducted between August, 1981 and December, 1982 at San Clemente Island, California. Southwest Fisheries Center Administrative Rep. LJ-87-23, La Jolla, CA. 47pp.

Oliver, C. W., M. S. Lowry, and L. M. Ferm. 1988. Pinniped studies conducted at San Clemente Island, California during 1983. Southwest Fisheries Center Administrative Rep. LJ-88-08, La Jolla, CA. 46pp.

Oliver, C. W. and J. B. Wexler. 1991. 1985 field studies on pinnipeds at San Clemente Island, California. Southwest Fisheries Center Administrative Rep. LJ-91-24, La Jolla, CA. 31pp.

Orr, R. T. and T. C. Poulter. 1965. The pinniped population of Año Nuevo Island, California. Proceedings of the California Academy of Sciences 32:377-404.

Perez, M. A. and T. R. Loughlin. 1991. Incidental catch of marine mammals by foreign and joint-venture trawl vessels in the U.S. EEZ of the North Pacific, 1973-88. NOAA Tech. Rept. NMFS-104. 57pp.

Perkins, P., J. Barlow, and M. Beeson. 1992. Pinniped and cetacean mortality in California gillnet fisheries: 1991. Int. Whal. Commn working paper SC/44/SM14.

Peterson, R. S., R. L. Gentry, and B. J. Le Boeuf. 1968. Investigations of pinnipeds on San Miguel and San Nicolas Islands. Unpubl. Exped. Rept., Univ. Cal., Santa Cruz. 15pp.

Pollard, E., K. H. Lakhani, and P. Rothery. 1987. The detection of density-dependence from a series of annual censuses. Ecology 68:2046-2055.

Reiter, J. and B. J. Le Boeuf. 1991. Life history consequences of variation in age at primiparity in northern elephant seals. Behav. Ecol. Sociobiol. 28(3):153-160.

Reiter, J., K. J. Panken, and B. J. Le Boeuf. 1981. Female competition and reproductive success in northern elephant seals. Animal Behavior 29:670-687.

Reiter, J., N. L. Stinson, and B. J. Le Boeuf. 1978. Northern elephant seal development: the transition from weaning to nutritional independence. Behav. Ecol. Sociobiol. 3:337-367.

Rice, D. W., K. W. Kenyon and D. Lluch. 1965. Pinniped populations at Islas Guadalupe, San Benito and Cedros, Baja California, in 1965. Transactions of the San Diego Society of Natural History 14:73-84.

Silverman. 1985. Some aspects of the spline smoothing approach to non-parametric regression curve fitting. Journal of the Royal Statistical Society, Series B. vol. 47.

Stewart, B. S. 1980. Historical and present populations of pinnipeds in the Channel Islands. In Potential effects of space shuttle sonic booms on the biota and geology of the California Channel Islands. San Diego State University Center for Marine Studies Technical Report 80-1. pp. 45-98.

Stewart, B. S. 1989. The ecology and population biology of the northern elephant seal, Mirounga angustirostris Gill 1866, on the southern California Channel Islands. Ph.D. Dissertation, University California, Los Angeles. 195pp.

Stewart, B. S. 1992. Population recovery of northern elephant seals on the southern California Channel Islands. In: D. R. McCullough and R. H. Barrett (eds.). Wildlife 2001: Populations. Elsevier Applied Science Press, New York.

Stewart, B. S. and R. L. DeLong. 1990. Sexual differences in migrations and foraging behavior of northern elephant seals. Abstract, Amer. Zool. 30(4):44A.

Stewart, B. S., and R. L. DeLong. (In press a). Post-breeding foraging migrations of northern elephant seals. In: B. J. Le Boeuf and R. M. Laws (eds.) Elephant Seals. Univ. Calif. Press, Berkeley.

Stewart, B. S., and R. L. DeLong. (In press b). Seasonal dispersion and habitat use of foraging northern elephant seals.

In: I. L. Boyd (ed.). Recent Advances in Marine Mammal Science. Symposia of the London Zool Soc., Oxford Univ. Press.

Stewart, B. S., B. J. Le Boeuf, P. K. Yochem, H. R. Huber, R. L. DeLong, R. J. Jameson, W. Sydeman, and S. G. Allen. (in press). History and present status of the northern elephant seal population. In: B. J. Le Boeuf and R. M. Laws (eds.) Elephant Seals. Univ. Calif. Press, Berkeley.

Stewart, B. S. and P. K. Yochem. 1984. Seasonal abundance of pinnipeds at San Nicolas Island, California, 1980-1982. Bulletin of the Southern California Academy of Sciences 83(3):121-132.

Stewart, B. S. and P. K. Yochem. 1985. Entanglement of pinnipeds in net and line fragments and other debris in the Southern California Bight. pp. 315-325 In: R. S. Shomura and H. O. Yoshida (eds.). Proceedings of the Workshop on the Fate and Impact of Marine Debris. NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-54.

Stewart, B. S. and P. K. Yochem. 1987. Entanglement of pinnipeds in synthetic debris and fishing net and line fragments at San Nicolas and San Miguel Islands, California, 1978-1986. Marine Pollution Bulletin 18(6B):336-339.

Stewart, B. S. and P. K. Yochem. 1990. Pinniped entanglement in synthetic materials in the Southern California Bight. pp. 554-561. In: R. S. Shomura and M. L. Godfrey (eds.). Proceedings of the Second International Conference on Marine Debris. NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-154..

Stewart, B. S. and P. K. Yochem. 1991. Northern elephant seals on the southern California Channel Islands and El Niño. pp. 234-243 In: F. Trillmich and K. A. Ono (eds.). Pinnipeds and El Niño. Springer-Verlag, Berlin.

Stewart, B. S., P. K. Yochem and H. R. Huber. 1985. Dispersion and migration of juvenile northern elephant seals born at San Nicolas and San Miguel Islands. Abstracts of the Sixth Biennial Conference on the Biology of Marine Mammals, November 22-26, 1985, Vancouver, British Columbia, Canada.

Stewart, B. S., P. K. Yochem, R. L. DeLong and G. A. Antonelis. In press. Trends in abundance and status of pinnipeds on the Southern California Channel Islands. Proceedings of the Third California Islands Symposium, 2 April 1987, Santa Barbara, California.

Stick, K. C., and L. Hreha. 1989. Summary of the 1988 Washington/Oregon experimental thresher shark gill net fishery. State of Washington Department of Fisheries Progress Report No.

275. 40pp.

Sydeman, W. J., H. R. Huber, S. D. Emslie, C. A. Ribic, and N. Nur. 1991. Age-specific weaning success of northern elephant seals in relation to previous breeding experience. Ecology 72(6):2204-2217.

Townsend, C. H. 1899. Notes on the fur seals of Guadalupe, the Galapagos, and Lobos Islands. The fur seals and fur-seal islands of the North Pacific Ocean. Part 3, pp. 275-278.

Trillmich, F. and K. A. Ono (Eds.). 1991. Pinnipeds and El Niño: Responses to Environmental Stress. Springer-Verlag, Berlin. 293pp.

Trillmich, F., K. A. Ono, D. P. Costa, R. L. DeLong, S. D. Feldkamp, J. M. Francis, R. L. Gentry, C. B. Heath, B. J. Le Boeuf, P. Majluf, and A. E. York. 1991. The effects of El Niño on pinniped populations in the eastern Pacific. pp. 206-218 In: F. Trillmich and K. A. Ono (eds.). Pinnipeds and El Niño. Springer-Verlag, Berlin.

Wexler, J. B. and C. W. Oliver. 1988. Pinniped studies conducted at San Clemente Island, California during 1984. Southwest Fisheries Center Administrative Rep. LJ-88-16, La Jolla, CA. 53pp.

Wild, P. A. 1985. Progress report: Central California gill and trammel net investigations (northern area), 1984. California Department of Fish and Game, Marine Resources Branch, Monterey, California 93940.

Wild, P. A. 1986. Progress report: Central California gill and trammel net investigations (northern area), 1985. California Department of Fish and Game, Marine Resources Branch, Monterey, California 93940.

(C_x) was computed for a population growing by the observed recent annual factor of increase, $\lambda = 1.0841$. [Fitted values for males differ from those given by Boveng (1988) due to the use of an improved fitting algorithm that resulted in a Siler fit that was closer to McCann's male life table].

Age (x)	FEMALES SES l_x	FEMALES FITTED l_x	FEMALES FITTED $\lambda^{-x}l_x$	FEMALES FITTED C_x	MALES SES l_x	MALES FITTED l_x	MALES FITTED $\lambda^{-x}l_x$	MALES FITTED C_x
1	1.000	1.000	.922	.269	1.000	1.000	.922	.307
2	.600	.600	.510	.149	.600	.634	.540	.179
3	.510	.510	.400	.117	.510	.514	.403	.134
4	.449	.449	.325	.095	.422	.417	.302	.100
5	.395	.396	.264	.077	.350	.337	.225	.075
6	.348	.350	.215	.063	.290	.273	.168	.056
7	.306	.308	.175	.051	.241	.220	.125	.042
8	.269	.271	.142	.041	.193	.178	.093	.031
9	.237	.238	.115	.033	.145	.142	.069	.023
10	.209	.208	.093	.027	.101	.114	.051	.017
11	.184	.180	.074	.022	.071	.090	.037	.012
12	.162	.154	.058	.017	.050	.070	.027	.009
13	.136	.129	.045	.013	.035	.053	.018	.006
14	.106	.106	.034	.010	.024	.039	.008	.004
15	.079	.083	.025	.007	.017	.027	.004	.003
16	.055	.061	.017	.005	.012	.017	.003	.002
17	.036	.040	.010	.003				
18	.022	.023	.005	.002				
19	.011	.010	.002	.001				
20	.004	.003	.001	.000				
TOTALS			3.431	1.000			3.009	1.000

[a]The stable age distribution', $C_x = \dfrac{\lambda^{-x}l_x}{\sum_{y=1} \lambda^{-y}l_y}$

Table 2. Estimated number of elephant seal pups born at California rookeries based on raw counts of number of alive and dead pups or on counts of live pups corrected for pup mortality.

Year	TOTAL	San Miguel Island	San Nicolas Island	Santa Barbara Island	San Clemente Island	Santa Rosa Island	Cape San Martin	Año Nuevo	South Farallon Islands	Point Reyes
1958	155	84[1]								
1959			71[1]							
1960										
1961										
1962								12[23]		
1963								23[2]		
1964	1032	878[3]	83[3]	11[3]	0[3]			32[2]		
1965			67[4]					60[2]		
1966			74[4]					75[23]		
1967								100[23]		
1968	1990	1624[24]	178[6]					143[23]		
1969			193[4]					188[7]		
1970			210[4]					247[7]		
1971			354[4]					301[7]		
1972	3306	2482[24]	428[8]	28[8]	0[8]			310[7]		
1973		3088[24]						367[7]	1[12]	
1974								395[7]	2[12]	
1975		3547[24]						480[7]	17[19]	
1976		4014[24]						605[7,31]	35[19]	
1977	6446	4760[24]	693[10]	74[24]	1[11]			690[7,31]	60[19]	
1978		5447[24]						814[23]	104[19]	
1979		5531[13]				0[13]		994[23]	133[19]	
1980	9247	6475[13]	1187[13]			0[13]		1173[23]	184[19]	
1981	10339	7272[13]	1546[13]			0[13]	3[21]	1353[23]	232[19]	
1982	11543	7376[13]	2312[13]		5[15]	0[13]	18[21]	1225[23]	292[19]	1[14]
1983	12282	8301[13]	1906[13]	25[16]	0[26]	0[13]	7[21]	1469[23]	367[19]	1[14]
1984	13668	9342[13]	2074[13]	80[16,33]	3[27]	0[13]	25[21]	1566[23]	475[19]	2[14]
1985	15243	10459[13]	2583[13]	97[16]	2[28]	2[13]	24[21]	1685[23]	447[19]	12[14]
1986	14723	9824[13]	2626[13]	73[16]	1[29]	0[13]	4[21]	1701[23]	360[19]	15[22]
1987	14985	10120[13]	2835[13]	75[32]	1[29]	2[13]	13[21]	1742[23]	434[19]	19[14]
1988	16555[25]	11083[18]	3154[18]	69[32]	0[30]	2[24]	13[21]	1524[23]	395[20]	20[14]
		11035[34]	3366[34]					1725[23]	393[20]	34[14]
1989	18395[25]	11292[18]	4751[18]	106[32]	0[30]	3[24]	67[21]	2001[23]	380[20]	44[22]
		11079[34]	4466[34]							
1990	18993[25]	12424[18]	4122[18]	69[32]	0[30]	23[18]	65[21]	1986[23]	396[20]	52[22]

Year	TOTAL	San Miguel Island	San Nicolas Island	Santa Barbara Island	San Clemente Island	Santa Rosa Island	Cape San Martin	Año Nuevo	South Farallon Islands	Point Reyes
1991	20972[25]	13191[18] 13884[34]	4597[18] 4082[34]	45[32] 94[34]	3[30]	83[18] 73[34]	263[21]	2248[23]	352[20]	81[22]

[1]Bartholomew and Boolootian 1960,as corrected for pup mortality by Stewart 1989
[2]Orr and Poulter 1965
[3]Odell 1971, as corrected for pup mortality by Stewart 1989
[4]Odell 1974, as corrected for unborn pups by Stewart 1989
[5]Le Boeuf 1977, as corrected for pup mortality by Stewart 1989
[6]Peterson, Gentry, and Le Boeuf 1968, as corrected for pup mortality by Stewart 1989
[7]Le Boeuf and Briggs 1977
[8]Antonelis, Leatherwood, and Odell 1981, as corrected for pup mortality by Stewart 1989
[9]Mate 1977, counts by DeLong corrected by Stewart 1989
[10]Le Boeuf and Bonnell 1980
[11]Le Boeuf and Mate 1978
[12]Huber et al. 1986
[13]Stewart 1989
[14]Allen, Peaslee, and Huber 1989
[15]Oliver and Lowry 1987
[16]Stewart and Yochem 1984, as corrected for pup mortality by Stewart 1989
[18]Lowry et al. 1992
[19]Huber 1987
[20]Sydeman, pers. data; Stewart et al., in press
[21]Jameson pers. data; Stewart et al., in press
[22]Allen pers. data; Stewart et al., in press
[23]Le Boeuf pers. data; Stewart et al., in press
[24]Stewart et al., in press
[25]Total values are based on averages of duplicate counts for some rookeries.
[26]Oliver, Lowry, and Ferm 1988
[27]Wexler and Oliver 1988
[28]Oliver and Wexler 1991
[29]Oliver 1991a
[30]Oliver 1991b
[31]Le Boeuf and Panken 1977
[32]Lowry, pers. data
[33]Lowry, Hansen, and Hawes 1987
[34]Stewart 1992

Table 3. Maximum counts of elephant seals during the breeding season in 1991. Values for the Farallones and Point Reyes represent the minimum number of distinct individuals that hauled out during the breeding season. The average fraction of males per pup (last column) is used in estimating the minimum population size for other rookeries for which total counts were not available.

	Adult Female	Adult Male	Unknown & Other Non-pup	Pups	Total	Adult Males per Pup
SAN MIGUEL ISLAND						
1 Feb 1991	11,898	2,065		13,063	27,026	0.158
SAN NICOLAS ISLAND						
2 Feb 1991	4,019	502	2	4,570	9,093	0.110
SANTA ROSA ISLAND						
1 Feb 1991	86	37		86	209	0.430
SAN CLEMENTE ISLAND						
11 Jan 1991			14	3	17	-
SOUTH FARALLON ISLANDS						
1991 Breeding Season	374	88	83	352	897	0.098
POINT REYES						
1991 Breeding Season	81	6	10	81	178	0.074
ANO NUEVO						
1 Feb 1991	2,122	378	9	2248	4,757	0.168
TOTAL	18,580	3,076	118	20,403	42,177	0.170

4. Results of regression of per-capita production on year.

Year	Births	Per-capita Production
1964	1032	0.1785
1968	1990	0.1353
1972	3306	0.1429
1977	6446	0.1278
1980	9247	0.1181
1981	10339	0.1165
1982	11543	0.0640
1983	12282	0.1129
1984	13668	0.1152
1985	15243	-0.0341
1986	14723	0.0178
1987	14985	0.1048
1988	16555	0.1111
1989	18395	0.0325
1990	18993	0.1042
1991	20972	

e= -0.00000598
err.= 0.00000202
rcept= 0.1638

uared= 0.404

mated births at zero production= 27,377
Bootstrap C.I.= (18,718 - 49,527)

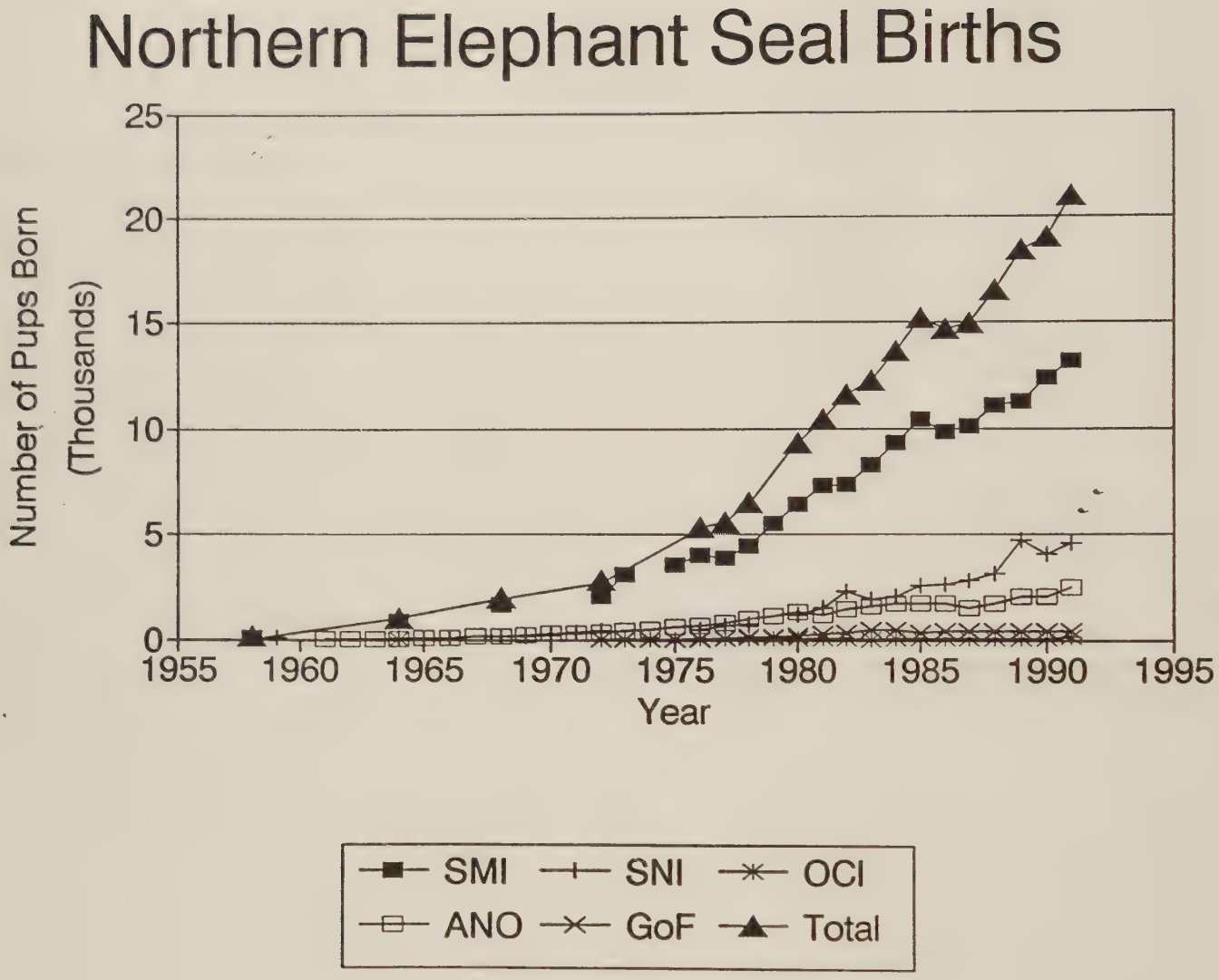
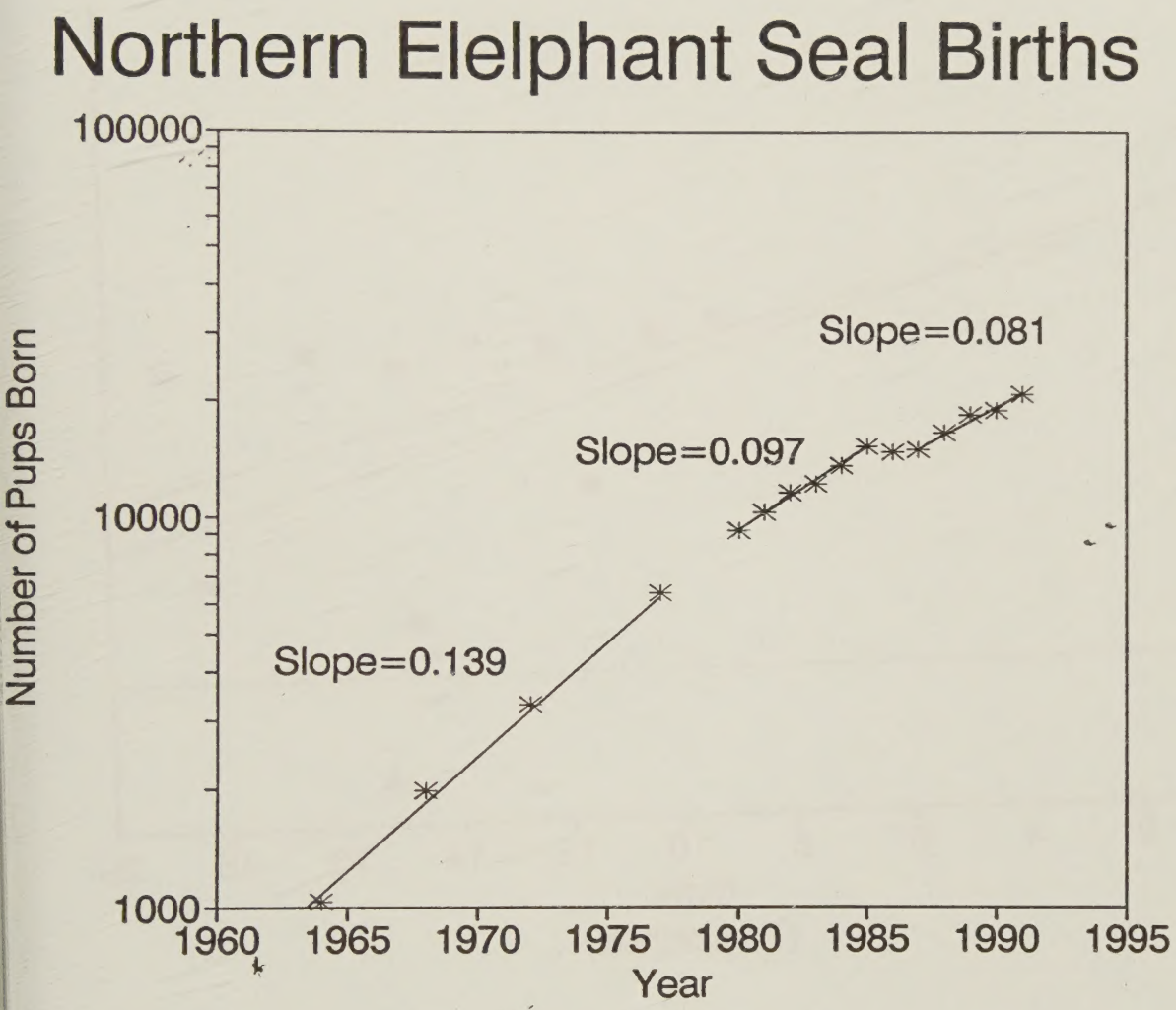


Figure 1. Estimated northern elephant seal births at San Miguel Island (SMI), San Nicolas Island (SNI), other Channel Islands (OCI), Año Nuevo (Island and Point) (ANO), and the Gulf of the Farallones (South Farallon Islands and Point Reyes) (GoF). Sources are cited in Table 2.



2. Natural logarithm of estimated births plotted against year, regression lines and slopes for the periods 1964-77, 1980-85, and

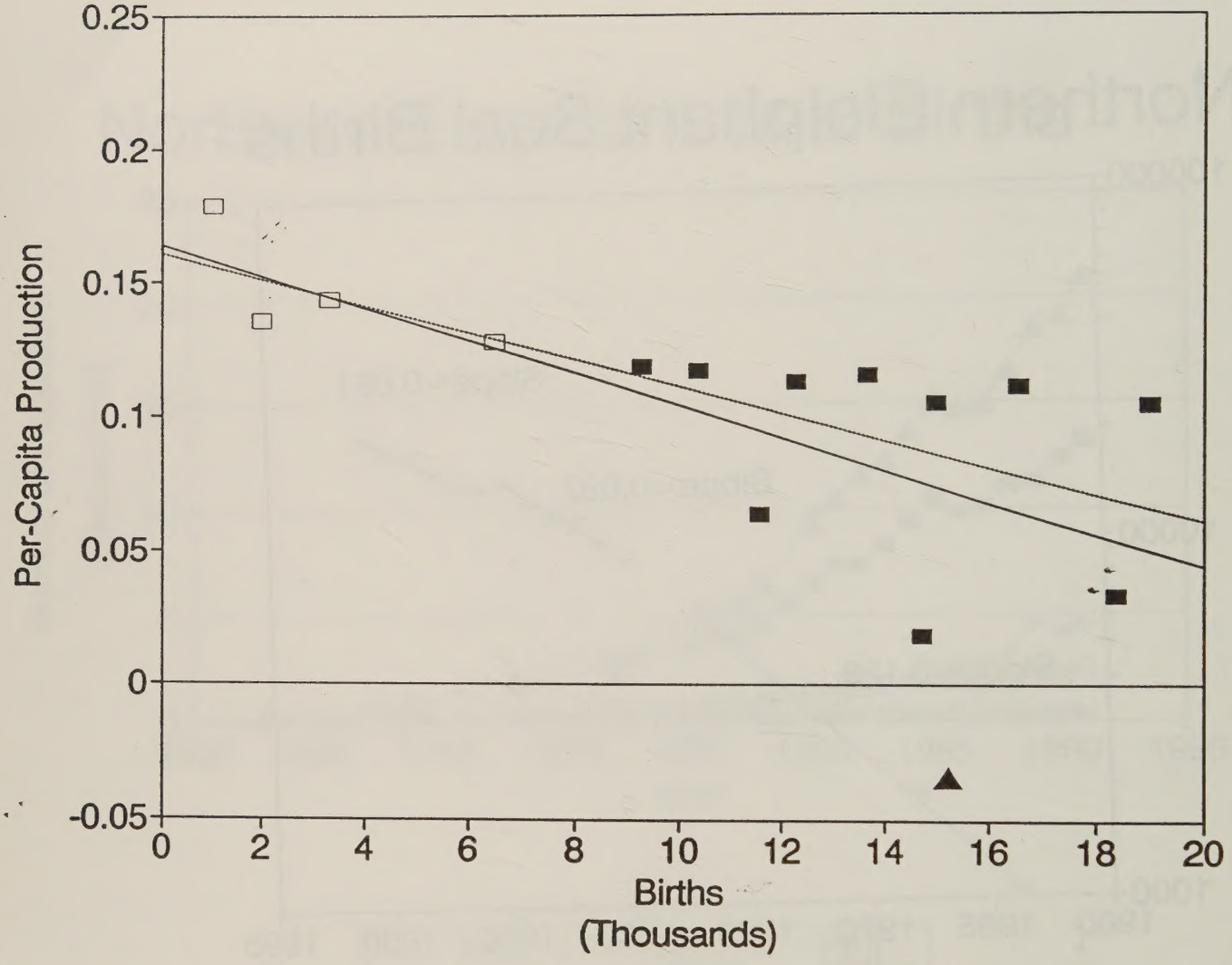


Figure 3. Cubic spline fit to the regression of per-capita production against estimated number of pups born. Solid squares and triangle indicate production rate estimates that were based on data from adjacent years. Open squares indicate production rates interpolated from non-adjacent years by assuming an exponential growth model. The smoothing parameter that minimized the cross-validation error resulted in the linear regression fit shown. Dashed line shows linear regression excluding the highly influential 1985/86 datum (solid triangle). Parameter values and goodness of fit statistics are given in Table 4.